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Research Article

Seed density and priority effects outweigh limiting similarity and diversity in contributing biotic resistance to invasion

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Abstract

Despite numerous ecological theories proposed to explain plant invasion dynamics, few studies have evaluated multiple mechanisms simultaneously within a single experimental framework. We conducted a greenhouse pot experiment to quantify the relative importance of five ecological factors – limiting similarity, diversity effects, priority effects, seed density, and soil carbon enrichment – on the invasion success of *Hypochaeris radicata*. Our experimental design tested competitive interactions between simultaneously establishing species rather than resistance from mature communities, representing realistic post-disturbance or post-control scenarios. Nine native species and five species mixtures were grown with the invader under controlled conditions, with treatments manipulating functional similarity (three functional groups based on longevity and woodiness), diversity (monocultures vs. four-species mixtures), arrival timing (3-week intervals), seed density (native:invasive ratios from 1:1 to 10:1), and soil carbon (sawdust amendments). Using structural equation modeling (SEM), we found that seed density (β = 0.487) and priority effects (β = 0.427) were the strongest determinants of invasion resistance. While functional similarity (β = 0.115) and diversity (β = 0.240) significantly contributed to invasion resistance, these effects were substantially weaker than those of seed density and priority effects. Soil carbon enrichment showed only marginal effects on invasion resistance (β = –0.081). Together, these factors explained 56.6% of the variation in competitive resistance. Our findings challenge the conventional emphasis on limiting similarity and diversity in restoring native communities resistant to invasion. Ecological restoration strategies should prioritize early establishment of natives at high seed densities rather than focusing primarily on functional trait matching or diversity enhancement.

Key words: Competitive resistance, diversity–resistance, functional group, *Hypochaeris radicata*, invasive plant management, limiting similarity, nitrogen limitation, priority effect, propagule pressure, seed sowing density, soil carbon enrichment, structural equation modeling

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Introduction

Invasive species are one of the leading causes of global biodiversity loss. They contribute to the degradation of natural ecosystems and the decline in native species diversity (Richardson et al. 2000; Roy et al. 2023). Invasive species often outcompete native flora, disrupt ecosystem functions, and alter habitat structures. A recent synthesis of the IPBES report estimated that invasive species are the sole driver of 16% of documented global species extinctions and contributed to 60%

of recorded global extinctions (Roy et al. 2023; Roy et al. 2024). These impacts persist because invasion outcomes are governed by multiple interacting assembly mechanisms (e.g., trait similarity, diversity, priority effects, propagule pressure, and environmental filtering), yet these mechanisms are rarely tested together in ways that identify which levers most effectively increase invasion resistance.

Ecological theory offers multiple explanations for why some native communities resist invasion while others fail. Among these, limiting similarity, diversity–resistance, priority effects, seed density (propagule pressure), and environmental filtering are widely recognized ecological mechanisms (Goldstein and Suding 2013; Byun et al. 2013; Tarsa et al. 2022; Farrell et al. 2022). Despite decades of empirical work, these mechanisms are typically examined in isolation or in paired combinations, often under distinct experimental designs and analytical frameworks (Byun et al. 2015; Berg et al. 2016; Lozano et al. 2023). This fragmented approach has limited our ability to determine their relative importance and to develop comprehensive invasion management strategies. Addressing this critical knowledge gap requires experiments that manipulate multiple mechanisms simultaneously and analytical approaches capable of quantifying their direct and indirect effects within a unified causal framework.

Limiting similarity provides one of the earliest and most mechanistically explicit explanations for invasion resistance. Rooted in MacArthur and Levins (1967), it predicts that species with greater functional similarity compete more intensely, reducing the likelihood of coexistence (Walder et al. 2019; Hess et al. 2020; Tortorelli et al. 2022; Grange et al. 2023). This theory is supported by studies showing that native species functionally similar to invaders can effectively reduce invasion success (Funk et al. 2016; Funk and Wolf 2016; Hess et al. 2020). The greater the similarity between native and invasive species, the less likely they are to coexist, as competitive exclusion becomes more pronounced with increasing functional similarity (Rodrigues et al. 2024). However, restoration applications based on limiting similarity remain challenging, partly because their effects are rarely evaluated relative to other co-occurring mechanisms such as diversity or priority effects (Hess et al. 2020; Singh and Byun 2023). This uncertainty motivates our first hypothesis that native species functionally similar to the invader will exert stronger competitive resistance.

The diversity–resistance hypothesis proposes a contrasting community-level mechanism whereby higher native species richness reduces invasion by increasing resource capture and niche complementarity (Elton 1958; Levine and D'Antonio 1999). Diverse communities can preempt space, light, and nutrients, leaving fewer opportunities for invaders to establish. Recent work suggests that diversity effects may depend not only on species number but also on functional composition and trait dispersion within communities (Wang et al. 2021; Mazzochini et al. 2023). Diversity is particularly important from a restoration perspective because it supports invasion resistance alongside broader biodiversity recovery goals (Cheng et al. 2024). Yet empirical evidence remains mixed, with some studies showing strong resistance effects and others finding weak or context-dependent outcomes depending on invader traits and environmental conditions (Wang et al. 2024a). These inconsistencies indicate the need to test diversity alongside other mechanisms, leading to our second hypothesis that species mixtures will show greater resistance to invasion than monocultures.

Priority effects, or the influence of species arrival order on community assembly, also play a critical role in competitive resistance (Young et al. 2017; Weidlich et al. 2021; Singh et al. 2024). Species that arrive first use available nutrients and

resources, thereby limiting the establishment and growth of later-arriving species. Early germination, rapid establishment, and high plant cover are indicators of strong priority effects (Byun 2022). Disturbance regimes common in invaded systems frequently disrupt native establishment while facilitating invader colonization, amplifying the importance of arrival timing (Pearson et al. 2023; Mazaleyrat et al. 2023). From a management perspective, manipulating arrival order through early native establishment may offer a low-cost intervention to enhance resistance. This forms the basis for our third hypothesis that early arrival of natives will enhance invasion resistance relative to simultaneous or delayed arrival.

Seed density, often conceptualized as propagule pressure, provides a quantitative dimension to competitive resistance. High densities of native propagules can intensify competitive effects, accelerate resource capture, and reduce the establishment probability of invaders (Tarsa et al. 2022). Empirical studies show that higher native seed densities or resulting biomass can suppress invasion, although effects may saturate at high densities due to density-dependent limitations (Le et al. 2024; Wang et al. 2024b). Despite its practical relevance – seed density is a directly manageable restoration lever – it is rarely evaluated simultaneously with functional similarity, diversity, or priority effects. We therefore hypothesize that higher native seed densities will increase invasion resistance, but with diminishing returns.

Finally, environmental filtering, particularly through soil nutrient modification, can mediate competitive outcomes by altering resource availability (Mangla et al. 2011; Kunstler et al. 2012; Beaury et al. 2020; Xu et al. 2022). Soil carbon amendments can influence competitive dynamics by altering nutrient availability, particularly nitrogen. Carbon additions typically stimulate microbial activity, leading to nitrogen immobilization as microbes incorporate the available nitrogen into their biomass (Blumenthal et al. 2003). This process can create nitrogen-limited conditions that may differentially affect native and invasive species depending on their nutrient requirements and competitive abilities under resource limitation (Iannone et al. 2009; Zhang et al. 2021). Carbon additions can reduce invasion success by enhancing microbial activity and nitrogen immobilization, potentially shifting competitive advantages (Xu et al. 2024). For example, invasive *Phalaris arundinacea* was suppressed by native wetland sedges, particularly in carbon-enriched soil (Perry et al. 2004). The nitrogen limitation induced by carbon enrichment may also benefit nitrogen-limited native plants by reducing nitrogen availability (Blumenthal et al. 2003). These findings motivate our fifth hypothesis that soil carbon enrichment can enhance invasion resistance by altering nutrient dynamics, particularly via nitrogen immobilization.

Despite the growing body of research on competitive resistance, most studies have focused on individual factors, with limited integration of multiple ecological theories and experimental manipulations within a single framework. This approach has hindered our ability to develop comprehensive strategies for invasive species management and ecological restoration. However, recent advances in structural equation modeling provide tools for evaluating complex interactions among various factors (Grace 2006; Grace et al. 2010; Grace et al. 2012). By simultaneously examining multiple drivers, structural equation modeling can provide a more integrated understanding of competitive resistance to invasion and inform more effective restoration practices.

Ecological theory offers several explanations for competitive resistance to invasion, including limiting similarity, diversity effects, priority effects, seed density

(propagule pressure), and environmental filtering (Goldstein and Suding 2013; Byun et al. 2013; Tarsa et al. 2022; Farrell et al. 2022). However, studies typically examine these mechanisms in isolation (Byun et al. 2015; Berg et al. 2016; Lozano et al. 2023). This fragmented approach has limited our ability to determine their relative importance and to develop comprehensive invasion management strategies. Here, we address this gap by experimentally manipulating key invasion mechanisms within a single framework and using structural equation modeling to quantify their relative contributions to invasion resistance.

We ask a central question in invasion ecology: when multiple mechanisms operate simultaneously, which factors exert the strongest control over invasion outcomes during competitive interactions? By simultaneously testing limiting similarity, diversity, priority effects, seed density, and soil modification, we quantify their relative and interactive contributions to competitive resistance. We expect that specific factors will disproportionately influence competitive resistance, allowing prioritization of the most effective restoration and invasion-management interventions. This integrative approach moves beyond mechanism-by-mechanism inference toward a hierarchical, decision-relevant understanding of invasion resistance.

Materials and methods

Target invader

Hypochaeris radicata is a perennial herbaceous plant in the Asteraceae family, introduced from Europe to the Republic of Korea. Its introduction was unintentional, arriving with grass seeds in the early 1980s (Kim et al. 2021). *Hypochaeris radicata* was designated as an invasive alien species in 2009 by the Ministry of Environment, Korea. Previous studies have reported its wide distribution on Jeju Island (Ryu et al. 2017; Kim et al. 2020; Park 2022; Son et al. 2023). *Hypochaeris radicata* occupies areas exceeding 10,000 m^2 and is expanding on Jeju Island, spreading through abundant seeds and propagules (Ryu et al. 2017). The species exhibits allelopathic effects, particularly against native species in the Gramineae and Leguminosae families (Kim et al. 2005; Son et al. 2023). Moreover, *H. radicata* is expected to threaten native biodiversity under climate change and human intervention (Jun et al. 2023), as it shows strong competitive ability under various environmental conditions (Mazaleyrat et al. 2023; Sobuj et al. 2024). High relative cover of *H. radicata* occurs in areas with frequent physical disturbances (Son et al. 2023). Additionally, Park (2022) reported that *H. radicata* expansion can be accelerated by mowing activities, complicating control efforts. *Hypochaeris radicata* is expected to thrive near urban areas with substantial human disturbance.

Overview of the experiment and common procedures

We designed a greenhouse pot experiment to evaluate the relative importance of five ecological factors in controlling invasion success: (1) functional similarity between native and invasive species; (2) community diversity; (3) priority effects through manipulation of arrival time; (4) seed density via different numbers of viable seeds; and (5) abiotic conditions through soil carbon enrichment. We defined invasion success here as the abundance of the target invader, *Hypochaeris radicata*, measured by stem density, plant cover, and plant height. The relative competition index (RCI) was then calculated as a composite measure of competitive resistance based on these

invasion success metrics. Nine native species and five species mixtures comprising these nine species were included. We considered longevity and woodiness for functional group classification, as these two traits proved most significant among the 10 tested functional traits. We induced competition between *H. radicata* (the target invader) and native species (both monocultures of nine species and five mixtures of four species). The experiment included 180 pots (approximately 30 cm diameter × 45 cm height) in a randomized complete block design with three replicates, maintained under controlled greenhouse conditions from February to October 2024. Temperature ranged from 10–30 °C and relative humidity from 40–70%. An automated irrigation system provided consistent water to experimental pots three times weekly. Our experiment tested biotic resistance to invasion under five experimental treatments: (1) species identity (functional trait similarity to the target invader *H. radicata*), (2) diversity (monocultures versus four-species mixtures), (3) priority effects (different arrival times of invasive and native species), (4) seed density (with different numbers of viable native seeds sown per pot), and (5) soil carbon (two levels of sawdust amendment). Each experimental treatment tested one of the hypotheses we proposed. To make the design easier to follow, below we describe the experimental methods under separate subheadings that align with each hypothesis or mechanism, while noting the common baseline conditions shared across treatments.

Selected species and functional classification

Native species were chosen based on multiple characteristics, including functional and habitat similarity with the target invader (grassland species; Suppl. material 1: table S1) and local seed availability. From 33 candidate species, we classified them by functional similarity and constructed a cluster dendrogram using the *FD* and *vegan* packages in R software (version 4.5.2) (R Development Core Team 2015).

Functional similarity was calculated using trait median values from the TRY database (Kattge et al. 2011). The functional traits included growth form, woodiness, longevity, seed mass, specific root length, specific leaf area, plant height, root/shoot ratio, relative growth rate, and leaf dry matter content. These functional traits are relevant to the leaf-height-seed plant ecology strategy scheme (Westoby 1998), the common core list of plant traits related to dispersal, establishment, and persistence (Weiher et al. 1999), and functional traits related to competitive ability and growth (Funk et al. 2008). While we initially considered all these traits, hierarchical clustering revealed that longevity and woodiness were the most influential in differentiating species groups in our dataset, aligning with their fundamental importance in plant ecological strategies. Consequently, we divided the 33 species, including invasive and native species, into three functional groups (Suppl. material 1: fig. S1): FG1 included annual species, FG2 comprised herbaceous perennials, and FG3 contained woody perennials. This classification allowed us to test whether invasion resistance was stronger when native species shared similar life-history strategies with the target invader (FG2).

All seeds were purchased in September 2023 and stored at 3 °C before germination testing. To select nine native species for our experiment, we tested seed germination rates for all 33 species from November 2023 to January 2024. Germination rates were determined to ensure that every experimental unit received the same number of viable seeds, except for seed density treatments. To measure germination rates, we placed 100 seeds on filter paper in Petri dishes with four replicates. Germination was induced at 10–20 °C with 50% moisture and a 14 h light/10 h

dark cycle. Distilled water was applied to each Petri dish three times weekly. After 5 weeks, we counted seedlings reaching 2 mm to calculate final germination rates (%) as the number of germinated seeds divided by the total seeds per Petri dish. We selected species with germination rates exceeding 5%. We intentionally selected three annual forbs, three perennial forbs, and three shrubs to maximize functional diversity while maintaining equal representation across groups (Byun et al. 2020a).

Hypothesis 1: Native species functionally similar to the invader will exert stronger biotic resistance

To test limiting similarity and diversity effects, we established nine monocultures of single native species representing the functional groups described above and induced competition with *H. radicata*. Biotic resistance was evaluated by comparing invader performance in each native monoculture relative to the invader-only control (see "Response variables" below).

Hypothesis 2: Species mixtures will show greater resistance to invasion than monocultures (diversity–resistance hypothesis)

To test diversity effects, we established nine monocultures (single native species) and five mixtures of four species. To isolate diversity effects from seed density effects, we maintained equal total viable seed density across all treatments (30 viable seeds per pot), meaning that in four-species mixtures, each species contributed approximately 7–8 viable seeds. This approach allowed us to test the effect of diversity per se, rather than conflating it with increased propagule pressure, which was tested separately in our seed density experiment. We acknowledge that testing only two diversity levels (monoculture versus four-species mixture) limits our ability to detect nonlinear diversity–invasion relationships or to determine optimal diversity levels. Our experiment specifically tests whether a mixture performs better than an average monoculture, rather than examining a continuous diversity gradient.

Hypothesis 3: Early arrival of natives will enhance biotic resistance relative to simultaneous or delayed arrival (priority effects)

To test priority effects, we sowed native seeds at different times (3-week intervals). We established three arrival scenarios: (1) native species arrived first, (2) native and invasive species arrived simultaneously, and (3) invasive species arrived first. All invasive seeds were sown on 22 March 2024; native seed mixtures for diversity treatments were sown on (1) 29 February, (2) 22 March, and (3) 11 April. In practice, the simultaneous arrival scenario corresponds to the baseline sowing date used for the identity/diversity treatments, whereas the priority-effect manipulation adds the earlier (native-first) and later (invader-first) sowing dates.

Hypothesis 4: higher native seed densities (propagule pressure) will increase biotic resistance

To test seed density effects, different numbers of viable native seeds were sown. Using mixtures, pots were established with different native:invasive ratios (1:1, 2:1, 4:1, 6:1, 8:1, and 10:1). For the 1:1 ratio, 30 viable seeds each of native and invasive

species were sown per pot. For the 2:1 ratio, 60 viable native seeds and 30 invasive seeds were sown per pot. This treatment tests both aspects of propagule pressure: the total number of propagules (seeds) and their relative abundance, which together influence competitive outcomes during establishment. Consistent with the overall treatment accounting (180 pots total), the 1:1 ratio represents the baseline sowing density (30 viable native seeds per pot) used in the identity/diversity treatments, and the density manipulation consists of the higher native:invader ratios (≥2:1).

Hypothesis 5: Soil carbon enrichment can enhance biotic resistance by altering nutrient dynamics, particularly via nitrogen immobilization

To test nitrogen limitation effects through carbon enrichment on invasion, we established 10 treatments. Two levels of carbon addition were tested (Perry et al. 2004): low (10 g sawdust from *Pinus densiflora* pot^{-1}, corresponding to 0.25 g $week^{-1}$ pot^{-1}) and high (50 g sawdust from *P. densiflora* pot^{-1}, corresponding to 1.25 g $week^{-1}$ pot^{-1}), with each pot containing 20,000 cm^3 of soil. Sawdust served as the carbon source for soil amendment and was applied on 22 January 2024, 2 months before seed sowing. Pine sawdust has a high C:N ratio (typically 200–500:1), which stimulates microbial activity and nitrogen immobilization when added to soil. While we did not directly measure soil nitrogen levels, the addition of high C:N organic matter is a well-established method for inducing nitrogen limitation (Blumenthal et al. 2003; Perry et al. 2004). We acknowledge that the 8-month duration of our experiment may be insufficient for complete sawdust decomposition but sufficient for initial microbial immobilization of nitrogen, potentially limiting our ability to detect long-term carbon-mediated effects on invasion resistance. The control for this treatment contained 30 viable seeds of the invader only.

Treatment structure, replication, randomization, and sowing

All treatments were replicated three times for a total of 180 pots: [1 control + 9 single native species + 5 diversity effect treatments (four species of natives) + 10 carbon addition treatments (four species of natives) + 25 density effect treatments (four species of natives) + 10 priority effect treatments (four species of natives)] × 3 replicates. While three replicates per treatment may appear limited for complex ecological experiments, this replication level is consistent with similar greenhouse studies examining multiple factors (Byun et al. 2020b; Lee et al. 2025). All pots were uniform in size (30 cm diameter × 45 cm height) and arranged in a randomized complete block design.

For baseline (non-priority) treatments, seeds were sown on the soil surface on 22 March 2024; all pots received water three times weekly (Monday, Wednesday, and Friday) using automatic water drippers throughout the experiment. Priority-effect treatments followed the staggered native sowing dates described above (29 February and 11 April) while maintaining the same invader sowing date (22 March).

Data measurement and data analysis

We measured growth parameters of both invasive and native species in October 2024, including stem density, plant cover, and maximum height. (1) Plant cover was measured as the percentage of pot area covered by plant canopy, (2) density was the number of stems per pot, and (3) height was the maximum plant length.

We also measured light availability above and below native canopies to calculate the light interception rate (%) using a light meter (Li-Cor LI-250A) with a quantum sensor. Values were automatically averaged over 10 s by the meter.

We used the relative competition index (RCI) as an indicator of competitive resistance to invasion. RCI was calculated using:

$$\textbf{Relative Competition Index(RCI)} = \frac{\mathbf{Y_{control}} - \mathbf{Y_{treatment}}}{\mathbf{Y_{control}}} \quad \text{equation 1}$$

where Y represents a performance parameter (plant cover, density, height, or biomass), and $Y_{control}$ and $Y_{treatment}$ are the performance values for *H. radicata* in the control and treatment pots, respectively. We calculated the average relative competition index, RCI_{avg}, as the mean of RCI_{cover}, $RCI_{density}$, and RCI_{height} because they were highly correlated (Suppl. material 1: fig. S2). An RCI_{avg} of 0 indicates no competitive resistance to *H. radicata*; values between 0 and 1 indicate some level of competitive resistance; values between –1 and 0 indicate facilitation of invasion by native communities.

Statistical data analysis

We used analysis of variance (ANOVA) for group comparisons. The randomized block design was analyzed using a generalized linear mixed model (REML; F-test). The generalized linear mixed model has a fixed effect of the tested factor of our experimental interests (e.g., diversity effect) and a random effect of blocks. It assumes a normal data distribution, and we checked this assumption whenever we ran the model and log-transformed the data if necessary. When significant effects were detected (alpha level = 0.05), Student's t-tests were used to compare mean values. Statistical significance was assessed using the F-statistic and P-value (<0.05). ANOVA and correlation analyses were performed using JMP software (version 13) (SAS Institute Inc. 2016).

Structural equation models were used to determine relationships among the five treatment factors (limiting functional similarity of species identity, diversity effect, priority effect, seed density, and soil carbon enrichment) and competitive resistance (RCI_{avg}) (Grace 2006). We chose SEM rather than simpler statistical approaches because it allows simultaneous evaluation of multiple predictors while quantifying their relative importance through standardized path coefficients, which was central to our research question regarding the hierarchical importance of invasion mechanisms. Additionally, SEM provides a framework for visualizing these relationships in an intuitive way that can inform management prioritization. We constructed a structural equation model to test hypothesized causal relationships among variables. The model structure was defined a priori based on ecological theory and previous studies. Exogenous and endogenous variables were specified according to our conceptual framework, and direct pathways were included where supported by prior evidence. While our experimental design did not include explicit interaction terms, SEM allows us to evaluate the relative importance of multiple predictors simultaneously, which was our primary research question. The SEM framework provides standardized path coefficients that quantify the relative strength of each factor's effect on invasion resistance, enabling prioritization of management interventions. The structural equation model was constructed with maximum likelihood estimation using the *sem* function in the *lavaan* package in R.

Results

Our experimental treatments produced significant variation in invasion resistance across treatments, with seed density and priority effects emerging as the strongest determinants of invasion success. While all five ecological factors except soil carbon enrichment significantly influenced invasion outcomes, their relative importance differed substantially.

Species identity and functional groups (limiting similarity)

The monoculture treatments showed significant differences in RCI_{avg} ($F_{8,16}$ = 12.69; P < 0.001). Among the tested species, *Ixeridium dentatum* showed the highest RCI_{avg} ($\bar{x}$ = 0.42), followed by *Achyranthes bidentata* ($\bar{x}$ = 0.19) and *Lespedeza bicolor* ($\bar{x}$ = 0.17) (Fig. 1a). The remaining species showed RCI_{avg} values close to 0 or below. Functional group identity significantly affected RCI_{avg} ($F_{2,22}$ = 3.45; P = 0.0494). Among the functional groups, FG2 (herbaceous perennials) showed the highest RCI_{avg} ($\bar{x}$ = 0.19; Fig. 1b). Since the target invader *H. radicata* also belongs to FG2, this suggests that functional similarity enhances competitive resistance to invasion. Functional trait dissimilarity (functional distance from the target invader) was negatively correlated with RCI_{avg} (r = –0.3759; P = 0.0533; Suppl. material 1: fig. S3).

Diversity effects

The diversity treatments (monoculture versus mixture of four species) significantly affected RCI_{avg} ($F_{1,38}$ = 20.98; P < 0.0001). Mixtures of four species had significantly higher RCI_{avg} values ($\bar{x}$ = 0.339) than monocultures ($\bar{x}$ = 0.07; Fig. 2). While our design only included two diversity levels, this significant difference suggests that even moderate increases in diversity can enhance competitive resistance during community assembly.

Priority effects

The priority treatment (arrival order through sowing time) significantly affected RCI ($F_{2,40}$ = 134.95; P < 0.001). RCI_{avg} was highest when native seeds were sown 3 weeks earlier than invasive seeds ($\bar{x}$ = 0.59), followed by simultaneous sowing ($\bar{x}$ = 0.15) and native seeds sown 3 weeks later ($\bar{x}$ = –0.04) (Fig. 3, Suppl. material 1: fig. S4).

Seed sowing density

The seed density treatment (number of viable seeds) significantly affected RCI (F = 9.88; P < 0.001). As the ratio of native to invasive seeds increased (from 1:1 to 10:1), RCI_{avg} increased significantly (Fig. 4, Suppl. material 1: fig. S4).

Soil carbon enrichment using sawdust

The soil carbon enrichment treatment (different amounts of sawdust) did not significantly affect RCI_{avg} ($F_{2,34}$ = 0.2429; P = 0.7857) (Fig. 5).

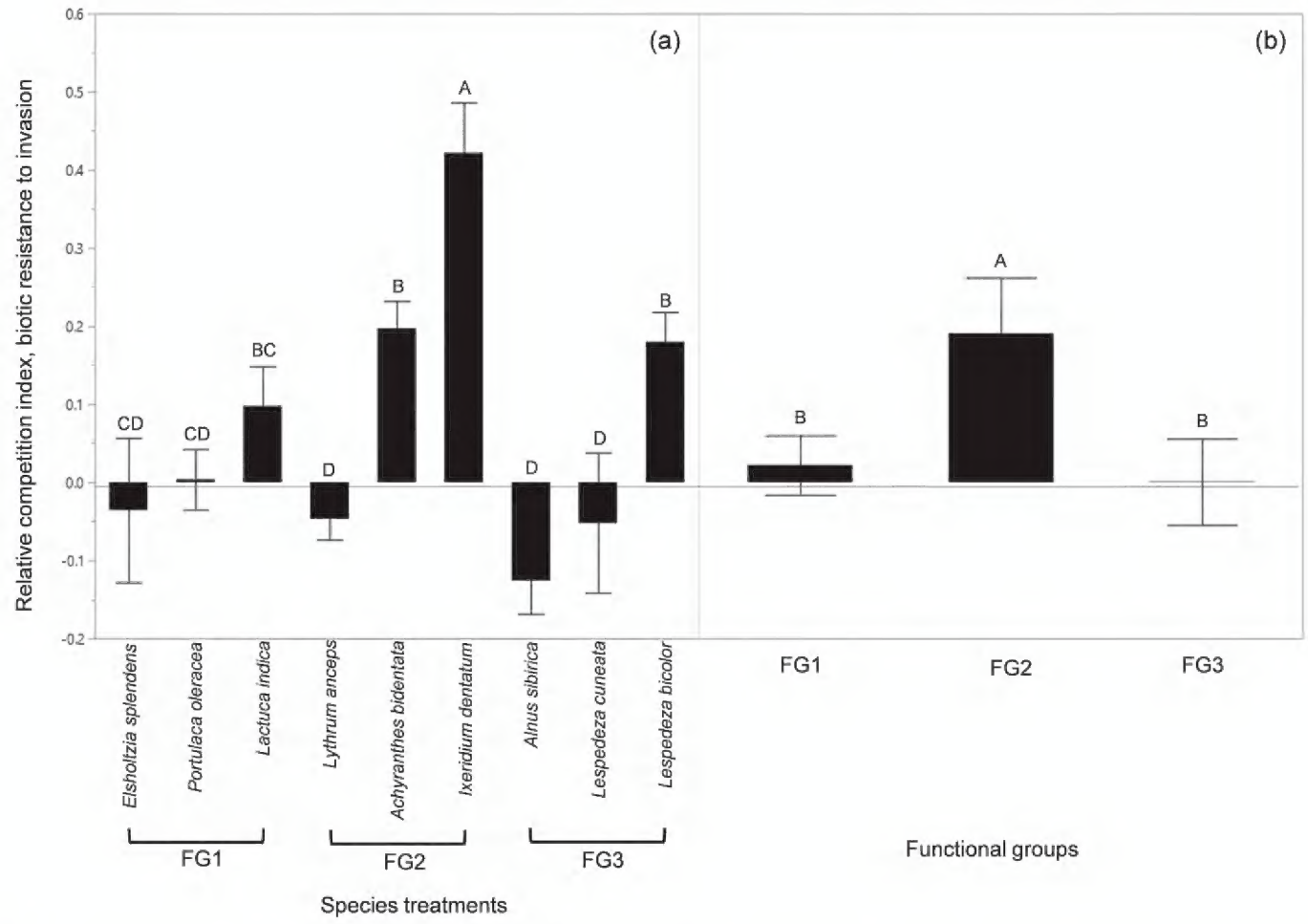

Figure 1. a. Effects of species identity and **b.** Functional group identity on competitive resistance to *Hypochaeris radicata* invasion, measured as the relative competition index (RCI). Higher RCI values indicate stronger invasion resistance. Functional groups: FG1 = annual forbs, FG2 = herbaceous perennials, FG3 = woody perennials. Data are shown as means ± SE, with n = 3. Bars sharing the same letter are not significantly different ($P > 0.05$, Student's t-test following ANOVA).

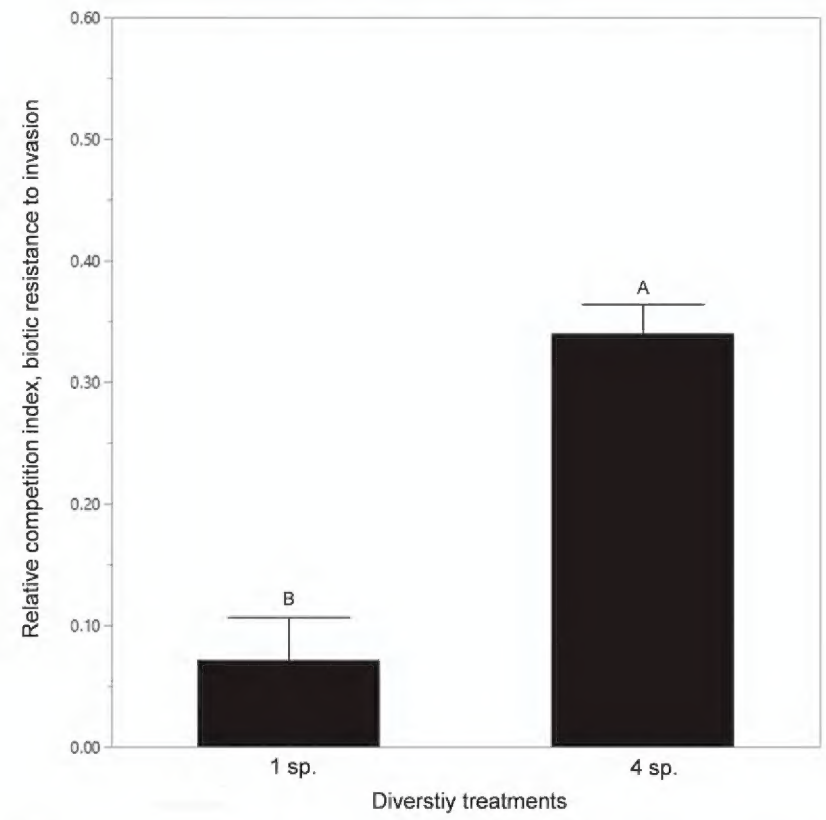

Figure 2. Diversity effects on competitive resistance to a *Hypochaeris radicata* invasion. Mixtures contained four native species from multiple functional groups; monocultures contained single native species. Data shown as means ± SE, with n = 3 for each bar. Different letters indicate significant differences ($P < 0.05$).

Growth parameters and light interception rate

We found significant positive correlations between native plant cover and RCI_{avg} ($r = 0.814$; $P < 0.001$), density and RCI_{avg} ($r = 0.683$; $P < 0.001$), canopy height and RCI_{avg} ($r = 0.479$; $P < 0.001$), and light interception rate and RCI_{avg} ($r = 0.480$; $P < 0.001$; Suppl. material 1: fig. S5).

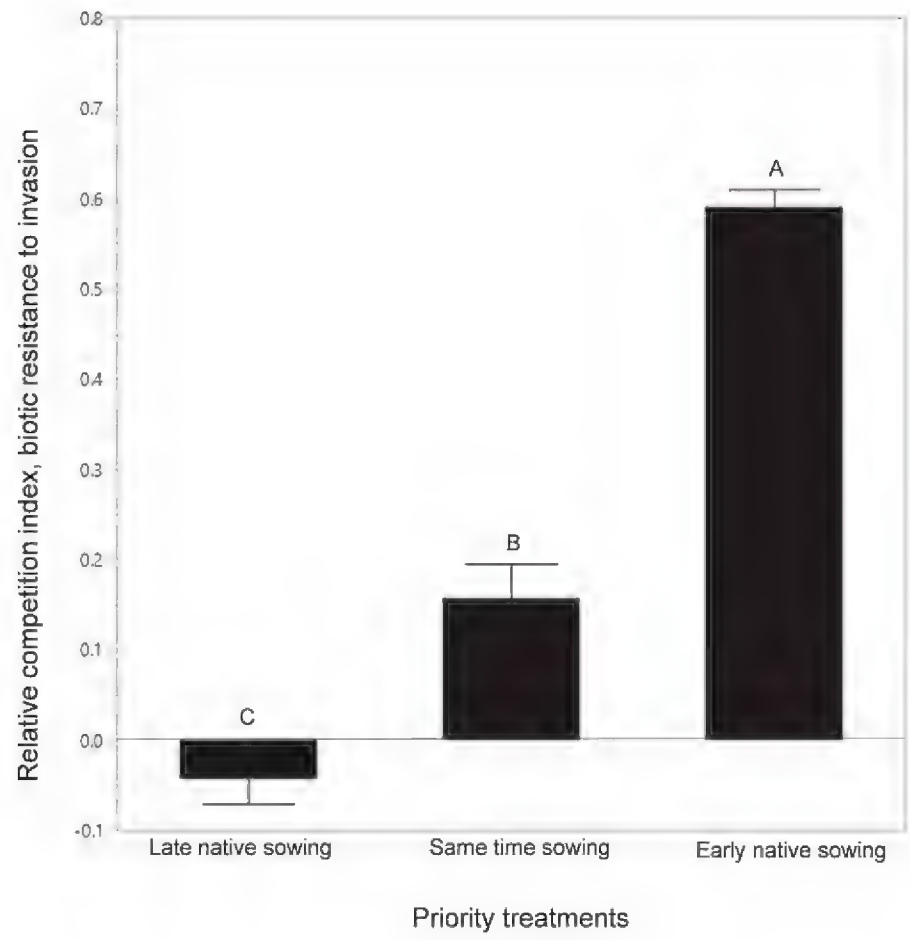

Figure 3. Priority effects on competitive resistance to a *Hypochaeris radicata* invasion. Treatments: "early native sowing" (native seeds sown 3 weeks before invader), "same time sowing" (native and invasive seeds sown concurrently), and "late native sowing" (invasive seeds sown 3 weeks before natives). Data are shown as means ± SE, with n = 3 for each bar. Different letters indicate significant differences ($P < 0.05$).

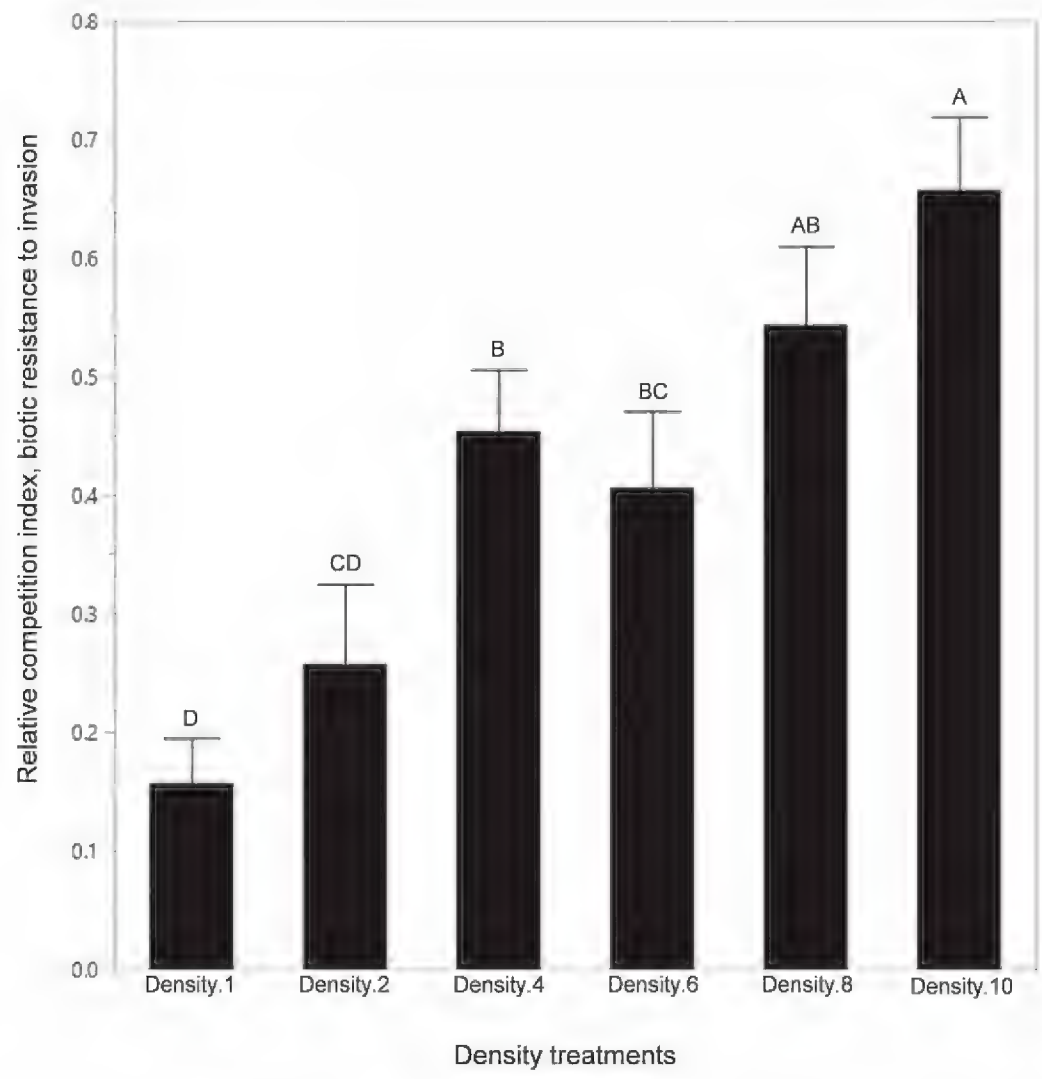

Figure 4. Seed density effects on competitive resistance to a *Hypochaeris radicata* invasion. The horizontal axis shows the ratio of native viable seeds sown, as follows: Density.1, original density (for the 1:1 ratio, 30 viable seeds of native and invasive species were sown per pot); Density.2, two times the native Density.1; Density.4, four times the native Density.1; Density.6, six times the native Density.1; Density.8, eight times the native Density.1; Density.10, ten times the native Density.1. Data are shown as means ± SE, with n = 3 for each bar. Different letters indicate significant differences ($P < 0.05$).

Structural equation model

The structural equation model revealed clear hierarchical relationships among factors controlling invasion resistance (Fig. 6). Seed density exhibited the strongest effect on competitive resistance to invasion (β = +0.487; P < 0.001), followed closely by priority effects (β = +0.427; P < 0.001). Community diversity showed a moderate positive effect (β = +0.240; P < 0.001), while functional similarity between native and invasive species had a significant but weaker effect (β = +0.115; P = 0.041). Soil carbon enrichment had only a marginally negative effect on invasion resistance (β = –0.081; P = 0.133). Together, these five factors explained 56.6% of the variation in competitive resistance to invasion (R^2 = 0.566), with seed density and priority effects accounting for the majority of the explained variance.

Discussion

Our integrated experimental approach demonstrates that seed density and priority effects exert substantially stronger control over invasion resistance than functional similarity or diversity, a finding that challenges the conventional emphasis in invasion ecology and restoration practice. By testing multiple ecological theories within a single experimental framework, we provide a quantitative hierarchy of mechanisms controlling the invasion success of *H. radicata*. The dominance of propagule pressure and arrival timing over trait-based mechanisms suggests that restoration strategies focused primarily on species selection may be less effective without adequate attention to temporal dynamics and seed density.

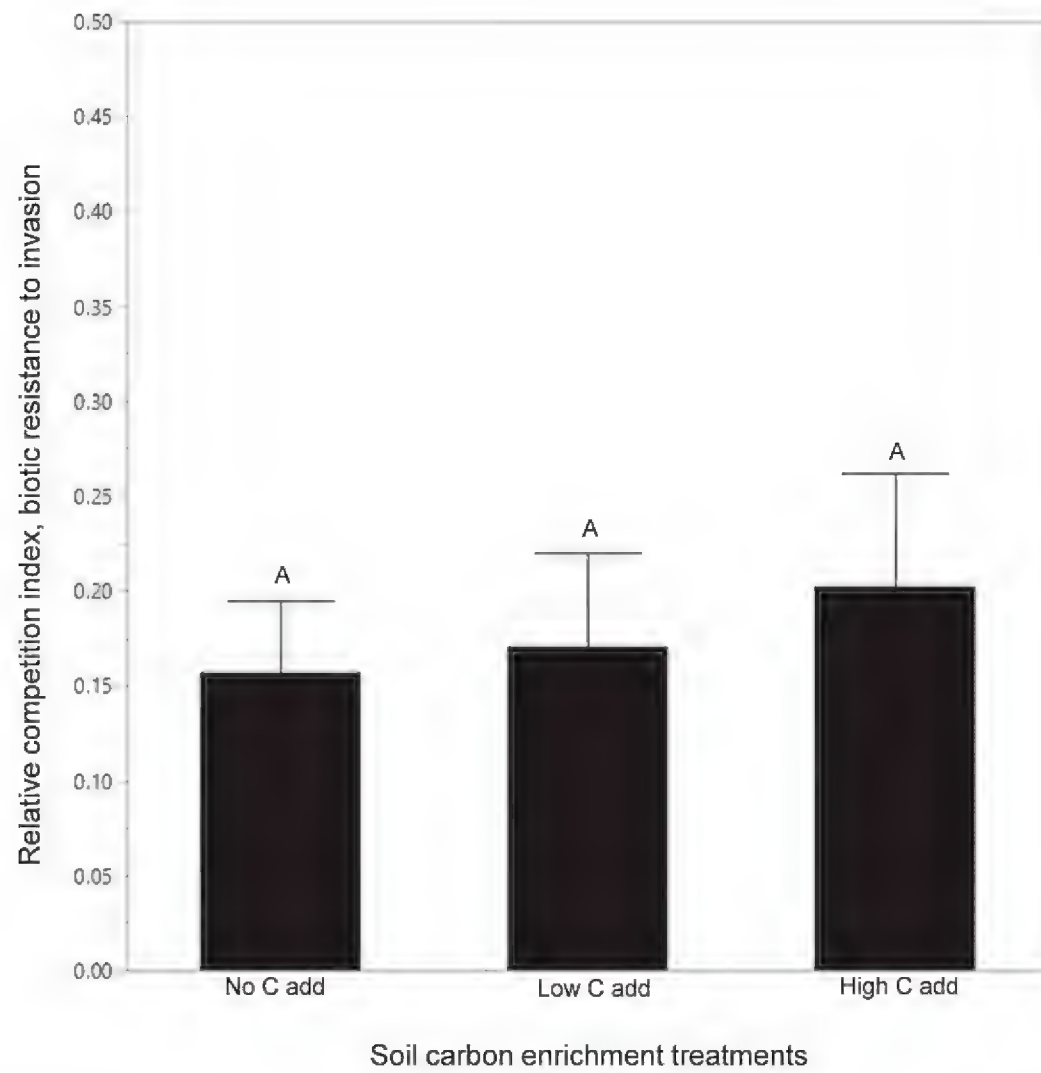

Figure 5. Effects of soil carbon enrichment using sawdust on the relative competition index, an indicator of competitive resistance to invasion. Low C add: 20 g of sawdust pot^{-1}; High C add: 50 g of sawdust pot^{-1} were applied. Data are shown as means ± SE, with n = 3 for each bar. The same letters indicate no significant differences (P > 0.05).

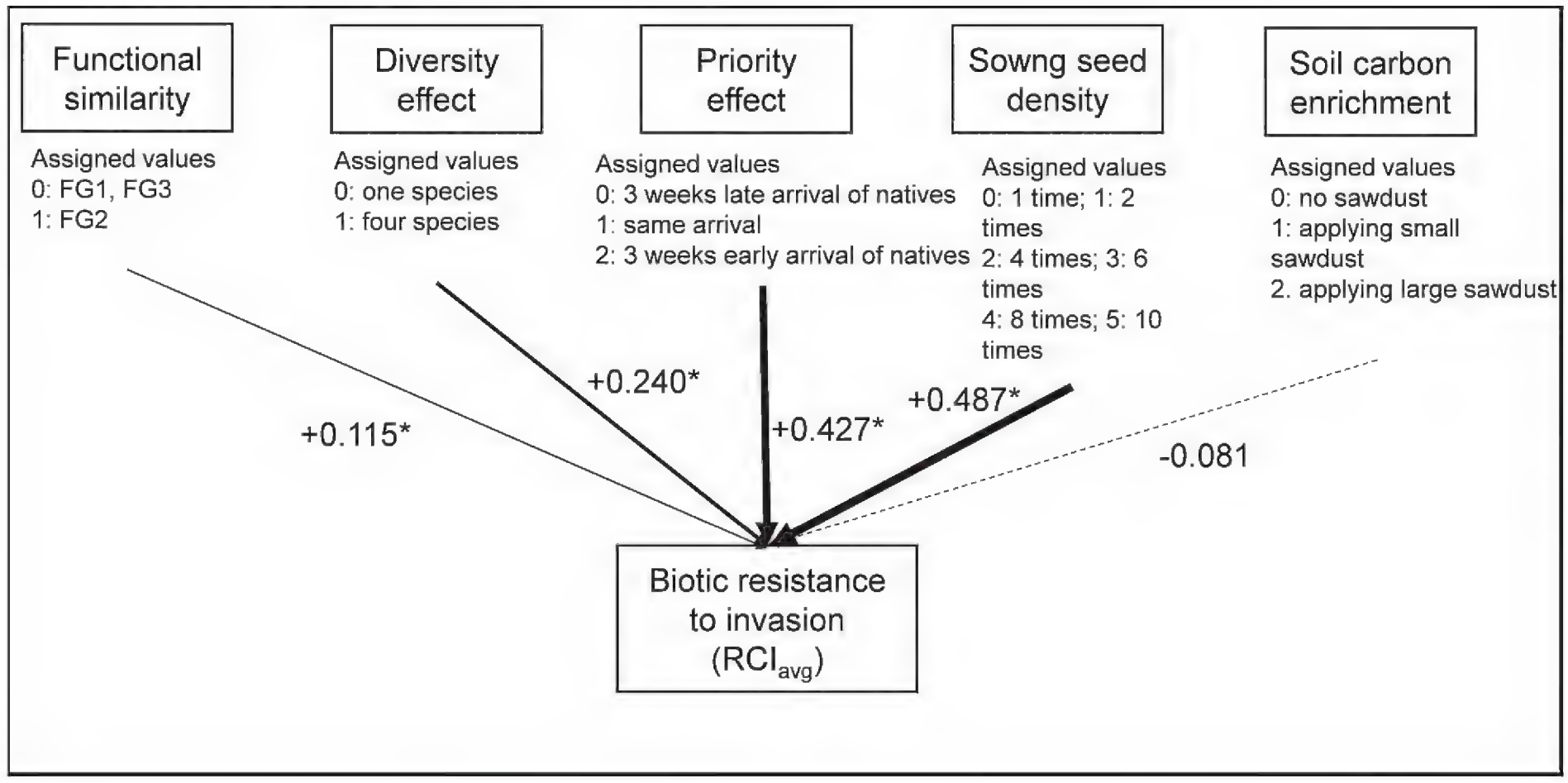

Figure 6. Structural equation model quantifying the relative importance of five ecological factors on competitive resistance to invasion. Values represent standardized path coefficients. Solid arrows indicate significant relationships ($P < 0.05$); dashed arrows indicate non-significant relationships ($P > 0.05$). Arrow thickness is proportional to effect size. Overall model $R^2 = 0.566$.

Our experimental design, while not testing classical biotic resistance from established communities, provides valuable insights into competitive dynamics during community assembly – a critical phase when many invasions occur following disturbance (Hobbs and Huenneke 1992) or eradication treatments (Lee et al. 2025). This approach has been validated in previous studies examining invasion dynamics during early succession (Byun et al. 2013; Yannelli et al. 2018). The competitive interactions we observed represent realistic scenarios in disturbed habitats where native and invasive species often establish simultaneously.

The herbaceous perennial functional group (FG2) was the most resistant to invasion among the three functional groups, though we observed species-specific variations within each functional group. These results support our first hypothesis about the importance of limiting similarity because the target invader (*H. radicata*) also belonged to FG2. *Lythrum anceps*, despite being in FG2, was least effective because it is a wetland-obligate species (wetland indicator status: OBW; Suppl. material 1: table S1), unlike other native species, and therefore did not establish well under the mesic soil conditions in our pot experiment. Our support for the limiting similarity hypothesis aligns with many previous studies (Funk et al. 2016; Walder et al. 2019; Hess et al. 2020; Tortorelli et al. 2022); however, other studies have reported inconsistent results (Price and Pärtel 2013). The relatively weak effect of limiting similarity in our study ($\beta = 0.115$) may be partially explained by our functional classification relying primarily on longevity and woodiness. While these traits emerged as most important in our clustering analysis, traits more directly related to resource acquisition (such as specific leaf area, leaf nitrogen content, or root/shoot ratio) may exert stronger effects on competitive interactions and invasion resistance (Funk and Wolf 2016). Future studies should explicitly test whether functional groups defined by resource-acquisition traits show stronger limiting similarity effects. Furthermore, applying limiting similarity in ecological

restoration may be challenging due to the requirement for a single predefined target invader rather than multiple target invaders and the potential lack of long-term suppressive effects (Hess et al. 2020).

While functional group identity significantly affected invasion resistance overall, we observed considerable variation in RCI_{avg} among species within the same functional group (Fig. 1a). For instance, within FG2 (herbaceous perennials), *Ixeridium dentatum* exhibited strong competitive resistance (RCI_{avg} = 0.42), while *Lythrum anceps* showed negligible resistance. Similarly, within FG1 (annual forbs), species-specific responses ranged from minimal to moderate resistance. This variation suggests that while functional group membership provides general insights into invasion resistance potential, species-specific traits and ecological adaptations remain important considerations for restoration applications (Feldman et al. 2024).

We found significant effects of diversity on competitive resistance to invasion. Specifically, mixtures of four native species showed significantly higher RCI_{avg} ($\bar{x}$ = 0.339) than monocultures ($\bar{x}$ = 0.07). This indicates that diverse communities more effectively suppress invasive species, supporting the diversity–resistance hypothesis and our second hypothesis. According to the diversity–resistance hypothesis, diverse communities utilize resources more efficiently, leaving fewer resources for invasive species to establish and thrive. Greater resource uptake and niche complementarity in diverse mixtures likely create a more competitive environment for invaders, enhancing competitive resistance (Henriksson et al. 2016; Byun et al. 2020a; Wang et al. 2021; Mazzochini et al. 2023). Consistent with extensive research, our findings support the importance of species richness in ecological restoration and invasive species management. Although monocultures may establish easily, they lack the functional redundancy and resource-use efficiency needed to effectively resist invasion. Conversely, diverse mixtures more effectively exploit available resources (Funk et al. 2016; Funk and Wolf 2016) and decrease community invasibility. Testing diversity across a continuous gradient in future studies would help identify potential threshold effects and optimal diversity levels.

Our findings demonstrate that the timing of native species arrival relative to invasive species significantly influences invasion outcomes. These findings support our third hypothesis and highlight the importance of priority effects in determining competitive resistance to invasion (Weidlich et al. 2021). Native species arriving several weeks before invaders likely gain a competitive advantage that hinders the establishment of later-arriving species (Weidlich et al. 2021; Torres et al. 2023; Halassy et al. 2023). Conversely, early invader establishment can reduce competitive resistance and compromise native community success. These findings align with previous studies and have important implications for plant invasion management and biodiversity conservation by emphasizing the need for early native species establishment and prompt invasive species removal (Yannelli et al. 2020; Weidlich et al. 2021; Torres et al. 2023). Temporal niche preemption plays an important role in restoring native communities with strong competitive resistance, as demonstrated by our early sowing treatments. Therefore, establishing native species before invasive species arrive, combined with long-term monitoring to prevent invasion, can improve the resilience of native communities to invasion. Additionally, minimizing disturbances that could eliminate native species' priority advantages is crucial, consistent with the disturbance hypothesis (Pearson et al. 2023).

The positive relationship between seed density and competitive resistance supported our fourth hypothesis and aligns with density-dependent competition the-

ory (Fronhofer et al. 2024). This theory suggests that at high densities, native species effectively utilize resources, including light, nutrients, and space, thereby reducing resource availability for invasive species. These findings align with previous studies showing that increasing seed densities of native species creates competitive conditions that reduce invasion success (Thomsen et al. 2006; Yannelli et al. 2018; MacLaren et al. 2019). Our treatment tested both the total number of propagules and their relative abundance, both of which are important components of propagule pressure that influence invasion outcomes (Miller et al. 2014). However, other findings suggest a potential threshold beyond which further density increases do not significantly improve competitive resistance (Nemec et al. 2013; Byun et al. 2015; Yannelli et al. 2018). This indicates that excessive seed densities may harm native species through intraspecific competition or resource limitations.

The non-significant effect of sawdust application on competitive resistance in our experiment cannot be interpreted as evidence against nitrogen-limitation effects on invasion, as we did not measure soil nitrogen levels to confirm whether nitrogen immobilization actually occurred. Without these critical measurements, multiple explanations remain possible: (1) nitrogen immobilization may not have occurred at all due to insufficient decomposition during the 8-month experimental period; (2) nitrogen limitation may have occurred but affected both native and invasive species equally, resulting in no net change in competitive outcomes; (3) the pot environment may not have adequately captured the complex soil microbial dynamics necessary for carbon-induced nitrogen immobilization; or (4) the invader *H. radicata* may not be particularly sensitive to nitrogen limitation. This represents a fundamental limitation of our study design. Future studies must include direct soil nutrient analyses throughout the experimental period to determine whether carbon amendments successfully induce nitrogen limitation and to test species with known differential responses to nitrogen availability.

This study provides valuable preliminary empirical data on the relative importance of multiple factors affecting competitive resistance to invasion during community assembly. The structural equation modeling results demonstrate that seed density and priority effects are the most important factors among those tested (Fig. 6), supporting our sixth hypothesis that certain factors would have disproportionate effects on competitive resistance. This result is consistent with recent studies that integrated multiple factors within a single research framework (Thomsen et al. 2006; Eschtruth and Battles 2009; Miller et al. 2014; Byun et al. 2020b; Lozano et al. 2023). We identified seed density and priority effects as key factors in shaping competitive resistance to invasion that have been underestimated in previous work. Several previous studies have also found that seed density or priority effects exert greater effects on invasion resistance than limiting similarity (Yannelli et al. 2018; Yannelli et al. 2020). These factors appear as important as diversity and limiting similarity, classically viewed as essential components of invasion resistance.

Study limitations and future directions

While our study provides valuable insights into the relative importance of invasion resistance mechanisms, we acknowledge several limitations that should guide the interpretation of our results and future research directions. First, our experimental design tests competitive interactions during co-establishment rather than resistance from established native communities. While this is a valid approach that has been used

successfully in previous studies (Byun et al. 2013; Byun et al. 2020b; Lee et al. 2025), it represents a specific ecological scenario – simultaneous colonization following disturbance or eradication treatments – rather than invasion into established communities. Future field experiments testing invasion into mature native communities would complement our findings and provide insights into classical biotic resistance.

Second, the 8-month experimental duration may be insufficient to capture longer-term ecological dynamics. Priority effects might shift over time as early-arriving species senesce or as perennial species reach their full competitive potential. Similarly, nitrogen dynamics following carbon addition likely require longer periods to fully manifest. We recommend that future experiments extend to at least 18–24 months to better capture these temporal dynamics.

Third, greenhouse conditions cannot fully replicate field complexity, including natural disturbance regimes, spatial heterogeneity, weather variability, and soil biota interactions. Field validation of our findings is essential to confirm their applicability to restoration practice.

Fourth, our diversity treatment included only two levels (monoculture vs. four-species mixture), limiting our ability to detect nonlinear diversity–invasion relationships. Future studies should test diversity across a continuous gradient to identify potential thresholds and optimal diversity levels for maximizing invasion resistance.

Fifth, our study evaluated invasion resistance mechanisms independently, but in natural systems, these factors likely interact in complex ways that could amplify or diminish their individual effects. For example, diversity effects might be most pronounced at intermediate seed densities, where facilitative interactions among species could outweigh competitive effects. Future factorial experiments should explicitly test these interactions.

The integration of disturbance dynamics with our findings provides an important framework for understanding potential interactions. Disturbance events, which commonly create invasion opportunities (Hobbs and Huenneke 1992; Pearson et al. 2023), can simultaneously reset priority advantages, reduce established biomass, and create resource pulses that alter competition dynamics. In this context, high seed density and functional diversity of natives might become particularly important following disturbance to rapidly occupy newly available niches before invaders become established.

Implications for restoration ecology and invasion management

The dominance of seed density and priority effects revealed in our study has direct implications for ecological restoration and invasive species management. Rather than focusing primarily on selecting native species with similar functional traits to potential invaders, our results suggest that practitioners should prioritize: (1) ensuring early establishment of natives before invasion occurs; (2) applying sufficiently high seed densities of natives to achieve rapid site occupancy; and (3) supplementing these approaches with attention to community diversity and functional composition.

Our findings help resolve inconsistent outcomes in restoration projects by demonstrating that trait- and diversity-based approaches may fail without adequate consideration of temporal dynamics and seed density. Specifically, restoration practitioners should consider the timing of restoration relative to likely invasion events, focusing on establishing native communities during windows of low invasion risk

and using high-density seed applications in areas at high risk of invasion. Where multiple potential invaders are of concern, incorporating functionally diverse natives remains important but should be secondary to ensuring adequate density and early establishment.

Future research should focus on factorial experimental designs that explicitly test interaction effects among factors, particularly across gradients of disturbance intensity and frequency. Research should test whether these relationships hold across different ecosystem types and spatial scales, as greenhouse studies may not fully capture landscape-level processes and disturbance regimes. Additionally, investigating how these factors interact with disturbance, which often creates invasion opportunities in natural systems, would further enhance our ability to develop resilient restoration strategies. Despite these limitations, our experimental results provide a useful preliminary roadmap for designing more effective restoration strategies that enhance invasion resistance through integrated management of multiple ecological factors.

We evaluated the relative contributions of five factors to the invasion success of *H. radicata*. We found that limiting similarity, diversity, priority effects, and seed density all influence competitive resistance to invasion, with little evidence for the effectiveness of nitrogen limitation through carbon enrichment via sawdust application in our experimental system. Our results demonstrate that considering a single factor is insufficient for integrated management and restoration. Our results particularly emphasize seed density and priority effects as key factors in competitive resistance to invasion, factors whose importance has been underestimated in the literature. Although future studies are needed to evaluate interactions among these factors, extend experimental duration, test multiple invaders, and validate findings under field conditions, this study provides a valuable step forward in quantifying the relative importance of multiple mechanisms affecting competitive resistance during community assembly. Field validation is essential before applying these findings to restoration practice.

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Additional information

Conflict of interest

The authors have no relevant financial or non-financial interests to disclose.

Ethical statement

No ethical statement was reported.

Use of AI

During the preparation of this work, the authors used Claude AI to improve the readability and language of the manuscript but not to generate any content. After using this tool or service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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Author contributions

CB contributed to the conceptualization, project initiation, and experimental design. DJ also contributed the experimental design. All authors contributed to the experiment setup and data collection. CB conducted statistical analyses and produced figures and tables. The initial draft of the manuscript was composed primarily by CB. DJ contributed sections of the Introduction, and KS contributed sections of the Discussion. KS subsequently revised the manuscript. All authors reviewed and approved the final version of the manuscript for submission.

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Data availability

The complete dataset is available through Figshare, ensuring full reproducibility and supporting global biodiversity research following FAIR data principles, https://doi.org/10.6084/m9.figshare.28473323.

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Supplementary material 1

Supplementary table and figures

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